

The Resting Position of *Cerodirphia speciosa* (Cramer), (Lepidoptera, Saturniidae): the Ritualization of a Conflict Posture

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(Plate I; Text-figures 1-4)

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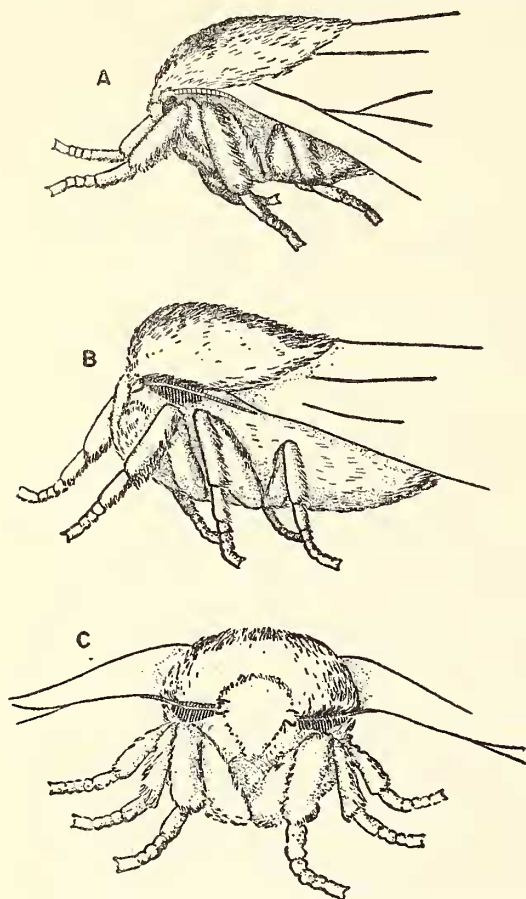
I. INTRODUCTION

RECENT work on the ritualization of signal movements in the vertebrates has stressed the role of conflict behavior in providing postures upon which selection may act to yield elaborately stereotyped displays; the final products of such evolutionary processes are frequently found to be freed or "emancipated" from the causal factors which mediated the ancestral conflicts. These evolutionary changes have recently been reviewed by Tinbergen (1952), Morris (1956, 1957), and Blest (1960.1). The position in the case of the invertebrates is less clear. Various authors have provided evidence to suggest that displacement behavior may occur in the invertebrates, and that in some cases, at least, such acts may have been incorporated into display behavior (Crane, 1949, 1952, 1955, 1957; Gordon, 1955), but to date there have been few detailed examinations of any particular instance. This paper will consider the usual adult resting posture of a hemileucine saturniid moth, *Cerodirphia speciosa* (Cramer), and will show that, while displacement behavior cannot be implicated in its evolution, it can be interpreted convincingly as an assimilated conflict posture. The essential background to this study will be found in a series of papers on saturniid behavior published elsewhere and in preparation (Blest, 1956; 1957.1, 2; 1958.1, 2; 1959; 1960.2; Bastock & Blest, 1958).

The typical resting posture of the hemileucine saturniids is shown in Text-fig. 1A. It is also found in the Citheroniinae (Text-fig. 1B, C). The antennae are held tucked against the sides of the thorax, just beneath the anterior margins of the folded wings. In this position they are to a greater or lesser extent concealed; the thin filiform antennae of female hemileucids are inconspicuous against thoracic hair of the same color. Furthermore, in those species which were studied from the closely related Citheroniinae (e.g., *Syssphinx*, *Adeloneivaia*, *Adelowalkeria*, *Adeloccephala* and *Eacles* spp.), the antennal scape is provided with hairs which at rest aid in concealing both the eye and the base of the antenna (Text-fig. 1B, C).

Unlike them, *Cerodirphia* when at rest holds the antennae above the wings, and lying along the dorsal surface of the thorax (Text-fig. 2A, B). They are pale and conspicuous. The difference between this position and that typical for the subfamily is superficially striking, and of a type for which saltatory mutation is frequently invoked as an explanation. It is similar to the posture which is typical for the group of saturnine genera which were formerly separated in the Attacinae (i.e., *Hyalophora*, *Philosamia*, *Rothschildia*, *Attacus* and *Epiphora*). It will be shown that the evolution of this resting posture can be explained in terms of the interaction between flight, settling and protective display behavior, of the selective forces which have modified the protective coloration of the species, and the complex of behavior patterns associated with it.

This work was made possible by a grant to the Smithsonian Institution, Washington, D. C., from the National Science Foundation, which allowed the field study of New World saturniid

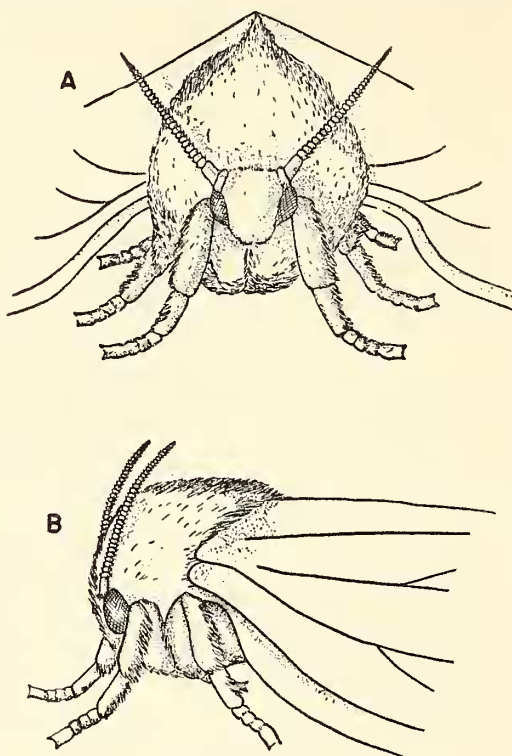


TEXT-FIG. 1. The antennal resting positions of hemileucine and citheroniine saturniids. A. *Dirphia* (*Periphoba*) *hircia*, from side. B. *Syssphinx molina*, from side. C. frontal view.

moths in Panama and in Trinidad from July, 1958, to January, 1959. In Panama, I am especially indebted to Dr. Martin Moynihan and Mrs. Adela Gomez for help extended in a variety of ways over a period of some five months. A stay of six weeks in the Arima Valley of Trinidad was made possible by the generous hospitality of the New York Zoological Society's Department of Tropical Research. I am most grateful to Dr. William Beebe, Miss Jocelyn Crane and Mr. Henry Fleming of the department for advice and assistance. The illustrations for this paper were prepared by Mrs. J. Emsley, from living specimens. I also owe a particular debt to Mr. Per Host for the loan of a 16 mm. ciné camera throughout much of this six-month period.

II. MATERIAL

Cerodirphia speciosa (Cramer) is an advanced member of the Hemileucinae (Michener,



TEXT-FIG. 2. The antennal resting position of *Cerodirphia speciosa* (Cramer). A. From side. B. frontal view.

1952), and belongs to the group of genera which includes *Ormiscodes*, *Molippa* and *Dirphia*. No species of *Ormiscodes* has been available for behavior study; members of the other two genera were freely available in both Panama and Trinidad. They were:

Molippa simillima Jones; Panama and Trinidad

M. latemedea (Druce); Panama

Dirphia (*Dirphia*) *avia* (Stoll); Trinidad

Dirphia (*Dirphiopsis*) *agis* (Cramer); Panama

Dirphia (*Dirphiopsis*) *eumedide* (Stoll); Panama and Trinidad

Dirphia (*Periphoba*) *hircia* (Cramer); Trinidad

Dirphia (*Periphoba*) sp. (not identified); Panama

Cerodirphia speciosa (Cramer); Trinidad

All the moths studied in the field were taken at 150-watt Photoflood lights in the laboratory clearings. A more detailed account of the two jungle habitats will be given in a later publication on the protective display behavior of some 50 species of hemileucine and citheroniine saturniids. The condition of the moths at capture indi-

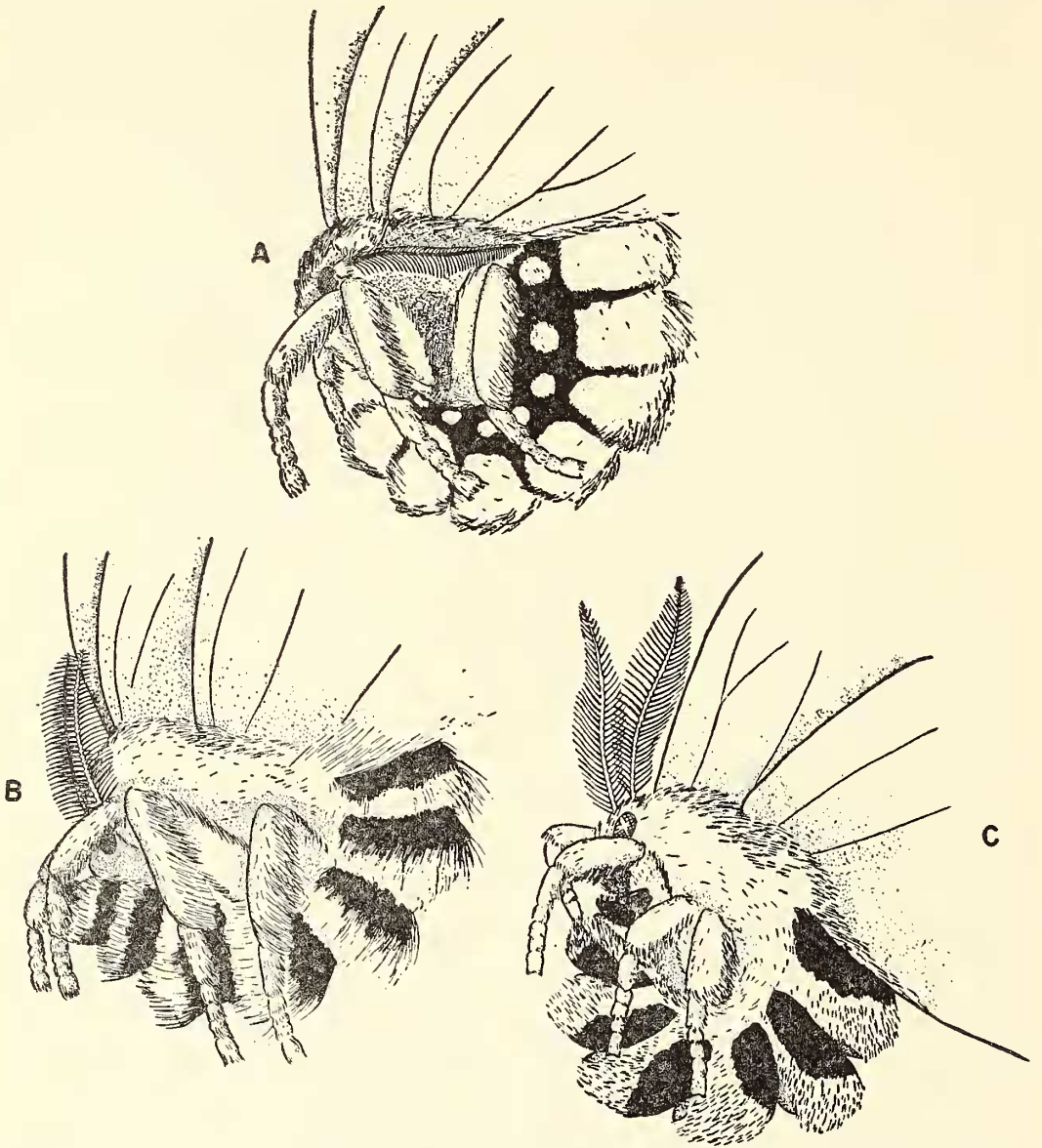
cated that the majority were probably taken on their first night of flight after emergence. Most moths were stored after capture at approximately 6°C. in a refrigerator, and observed in the course of the following day. Refrigeration at this temperature does not impair the normal behavior of saturniids when they are returned to room temperature. The detailed laboratory study of *Automeris aurantiaca* (Weymer) which provides the background against which the present material will be interpreted was conducted in London with two purchased stocks originating from an unknown Brazilian source (Bastock & Blest, 1958; Blest, 1958.1; 1959.1). The settling and display behavior of representative species was recorded on 16 mm. Kodachrome film at 24 frames/sec. and analyzed in the laboratory.

III. THE BEHAVIOR PATTERNS AND THEIR INTERACTIONS

C. speciosa is an aposematic species, with almost unicolorous dusty pink fore and hind wings, ornamented with a few whitish stripes, a black-and-white-banded abdomen bearing an orange anal hair tuft, and with a perceptibly unpleasant odor. Correlated with these morphological features is a striking absence of organized protective display behavior. Species in the allied genus *Dirphia*, belonging to several different subgenera (*Dirphia*, *Periphoba*, *Dirphiopsis*), are also distasteful (Blest, in prep.) but are to different degrees cryptic when at rest; their aposematism is confined to abdominal striping which is evident neither at rest nor in flight. Tactile disturbances applied to resting moths, or even to moths in flight, elicit a Type II Sustained Static Display (Blest, 1957.2) in which the wings are strongly elevated and adpressed dorsally, while the abdomen is tightly curled, exposing the aposematic banding patterns; these postures are normally maintained for periods of several minutes (Text-fig. 3A, B, C.). Yet only exceptional individuals of *Cerodirphia* will perform sustained displays of this type (Pl. I); in almost all specimens of either sex, display is absent, and tactile disturbance stimulates immediate weak fluttering flight, in which both the pink wings and the brilliantly colored abdomen are well in evidence, and the characteristic odor is dispersed in a dust of loose scales and fragmented hairs. Even at tropical temperatures, the flight of the more heavily-built saturniids tends to be poorly efficient when started from rest without a previous period of "warming up" by "shivering" (Krogh & Zeuthen, 1941). *Cerodirphia* rarely shivers and the threshold for the tactile release of flight is exceptionally low. In fact, this ready excitability of flight responses is a sufficient explana-

tion for the absence of display, for there is evidence that the balance between the two tendencies to display and to fly, where both are released by the same tactile stimuli, is mediated by reciprocal inhibitory relationships between the two systems controlling them (Bastock & Blest, 1958; Blest, 1958.2); thus, a tactile stimulus results in the simultaneous activation of both systems, which is resolved in favor of one or other of them. It follows that a disproportionately low threshold and high excitability in one system, in this case flight, will result in the total suppression of the other, display. Such a disproportion, built into the genetic constitution of the species, could clearly be responsible for the characteristically weak protective display behavior of *Cerodirphia*.

But a shift of this kind in the excitability of flight responses would have another consequence, which may be put to experimental test. For this to be understood, the nature of the settling responses of the Hemileucinae must first be considered, together with the way in which they are linked to flight performance and flight excitation. When hemileucine moths settle into the rest position from any other activity, they perform rhythmic, side-to-side oscillations by means of flexion and extension movements of the legs; at the same time the head performs side-to-side movements in phase, rotating around the long axis of the body (Bastock & Blest, 1958). The number of oscillations performed by moths of a given age shows a direct linear relationship to the duration of the preceding flight performance (Blest, 1958.1). The optimal score which may be yielded by a given flight performance may be reduced, however, by close proximity between the flight response and the act of settling (Bastock & Blest, 1958), and by procedures which act to build up an excitatory state in the flight system (Blest, 1960.2). Such states may typically be produced by the action of a series of tactile stimuli individually subliminal for the release of flight; sufficiently long-continued they will summate to release flight, but in the early stages of summation, the settling response, if tested, is found to be in the course of undergoing extinction (Blest, 1960.2). The reduced rocking responses so produced tend, particularly in the later stages of their decremental course, to have a characteristic feature; the antennae are not wholly retracted into the rest position, and the steady decrease in the amplitude of the rocking movements does not continue to zero (Text-fig. 4). Both these basic relationships between flight and the settling response are controlled by central nervous interactions which are independent of all afferent pathways other than those implicated by the release of flight (Blest, 1959).

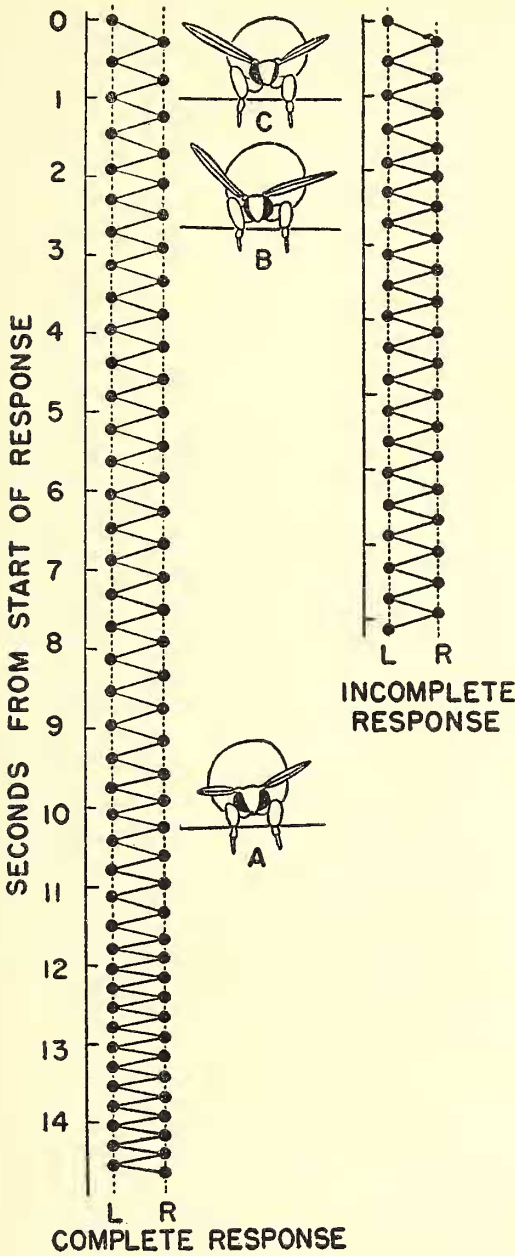


TEXT-FIG. 3. The full protective display postures of some aposematic Hemileucinae. **A.** *Dirphia* (*Dirphopsis*) *eumedide*; note that the small, narrow antennae lie along the thorax beneath the wing-bases. **B.** *Dirphia* (*Dirphia*) *avia*; the antennae are larger, light in color, and elevated during display. **C.** *Dirphia* (*Periphoba*) *hircia*; the large, lemon-yellow antennae are strongly elevated throughout display, and the abdominal tip is orientated towards the uppermost side of the moth.

Now, from *Automeris aurantiaca* which have flown sufficiently long to yield rocking response strengths of between 10 and 20 oscillations, it is rarely that a single tactile stimulus will elicit immediate overt flight. Thus, if the strength of the rocking response is tested at intervals of several minutes, it is found to be stable; a single test, although it involves from 2 to 3 seconds of forced, tethered flight (see below), is not suf-

ficient to raise the basal level of flight excitation.

It might be supposed, then, that the procedure used to test the strength of the rocking response of *Automeris aurantiaca*, in which a de-alated preparation from which the abdomen has been removed is replaced on a substrate after a standard 2 to 3 seconds of forced tethered flight, would fail to reveal a stable strength of the rocking response for *Cerodirphia* after any in-



TEXT-FIG. 4. Diagram to illustrate the co-ordination of an incomplete settling movement. At the left the timing of a complete settling movement is shown. The points represent the extreme left and right positions reached in successive swings of the oscillation. The amplitude changes are not represented. The diagram is derived from a film record of *D. (Periphoba) hircia*. Note that at the point marked **A** the antennae are still not fully retracted. In the case of an incomplete response, the antennae remain elevated in the positions shown at **B** and **C** in the diagram.

interval of rest. The test procedure itself would throw the labile flight system into an unstable state. Support for this latter assumption may be found in the observation that resting *Cerodirphia* in closed containers under diffuse daylight commonly indulge in sudden "spontaneous" bursts of fluttering, either to stimuli so small as to escape detection or, less probably, in their absence; whichever is true, it would seem likely that *Cerodirphia* lacks a stable level of activity in the flight system.

A number of fresh male individuals of *Cerodirphia speciosa* taken at light were treated in the following way: it was firstly assumed that the flight performance which brought them to light after emergence was adequate to yield a rocking response of the appropriate strength. No special period of forced tethered flight, therefore, was imposed upon them. Some 8 to 12 hours after capture they were de-alated, the abdomen removed, and, after five minutes for recovery (an interval known to be sufficient in the case of *A. aurantiaca*), tested for the strength of the rocking response at intervals of 15 minutes from the time of first testing. Preliminary tests showed that the procedure followed with *A. aurantiaca*, which imposed 2 to 3 seconds of forced tethered flight before each test, merely served to excite sustained flight responses from *Cerodirphia*. For this reason, the six males whose performance is recorded in Table 1 were simply lifted with forceps until their tarsi were all just out of contact with the substrate, and then immediately replaced on it and the strength of the settling response recorded. The results are clear; none of the moths achieved a stable rocking response. Thus, one further point may be made about the settling behavior of *Cerodirphia*: the settling responses must be predominantly incomplete, a fact which is masked by the aberrant antennal rest-position.

The source of this position may now be interpreted through a comparison of the role of the antennae in the aposematic displays of related genera. Primitively, as in *Molippa* (and indeed, in those distantly related or unrelated genera which have evolved similar displays through convergence, such as *Hylesia*, *Citheronia*, *Adelowalkeria* and *Adeloneivaia* spp.), the antennae are inconspicuously colored and during display remain, with the legs, tightly adpressed against the thorax. This condition, which is also found in *Dirphia* (*Dirphiopsis*), is illustrated in Text-fig. 3A. Through *Dirphia* (*Dirphia*) (Text-fig. 3B) to *Dirphia* (*Periphoba*) (Text-fig. 3C) there is found a succession in which the antennae increasingly contrast with the ground color of the thorax and wings and during display become ele-

TABLE I. INSTABILITY OF THE ROCKING RESPONSE OF *Cerodirphia speciosa*.

Each individual was retested at intervals of 15, 30, 45, 60, 75, 90, 105 and 120 minutes after the first response at 0 minutes. Read horizontally, the figures give successive rocking scores.

Time in minutes	0	15	30	45	60	75	90	105	120
a	16	12	10	15	4+f	0+f	16	7	4
b	0	5	7	4	4	13	4	6	0
c	1	*	*	12	6	15	4	3	0
d	*	9,9	14	13	*	5	7	*	0
e	*	3	1	14	0	7	12	2	3
f	*	*	5	*	*	0	7	4	0

* = no settling obtained within 5 minutes of test.

f = test followed by spontaneous flight behavior within 5 minutes.

vated until in *D. (Periphoba) hircia* they are large, bright lemon-yellow and lie parallel and slightly anterolaterally to the fore-margins of the elevated forewings throughout display. Comparison with the few specimens of *Cerodirphia* whose low flight excitability allowed the appearance of transient display, showed that the antennal position was identical.¹ The relevant behavior patterns of the eight species are summarized in Table 2.

Numerous observations have been made on the display and settling behavior of *D. (Periphoba) hircia*. The head rotations in this species are exceptionally vigorous and easily traced, and the strength of the rocking response is unusually high; responses of over 40 oscillations are common in moths even when they are more than 24 hours old. An individual of *A. aurantiaca* of the same physiological age would have to fly for more than 60 minutes to achieve the same score, and flight responses would in nearly all individuals be extinguished long before. Very frequently, the head rotations of *D. hircia* are commenced at the same time that the wings are depressed from the display position, and this is particularly so when the strength of the rocking response is high. For rocking responses of a strength of 40 oscillations or more, it may be found that as many as 15 oscillations have been performed by the time that the wings are parallel to the substrate, usually with the antennae still strongly elevated and above them. Now, it has been noted that incomplete rocking responses start normally, but that the terminal stage of the complete act, in which the antennae are fully retracted, the amplitude declines to zero and the

speed is most markedly accelerated, is, as it were, amputated from the rest of the response. Thus the effect of an increased excitability of flight would be to increase the proportion of incomplete settling responses after display, so that a more-or-less elevated position of the antennae would become the predominant resting state. There is no doubt that there is strong selection pressure for the stabilization of antennal resting positions, if only because they are found to be so highly specific to particular taxonomic groups, and so markedly stereotyped. The most plausible explanation of the resting position of *Cerodirphia speciosa*, then, assumes that it has arisen adventitiously as a consequence of the radically decreased flight threshold and the mode of protective display, and has subsequently been stabilized by selection. The fact that the whitish antennae provide a contrast against the pinkish-brown thoracic hair and so add to the aposematic coloration may explain why selection has preferred the incomplete settling response over that of normal settling from flight.

IV. DISCUSSION

The conflict situation basic to this example is quite clearly rather different from the cases of displacement activity which have been previously described for the invertebrates. Where these are critically acceptable, they concern situations in which two incompatible activities are simultaneously aroused, and the outcome of their competition is the appearance of a third activity, generally in a rather aberrant motor form, which is ecologically or ethologically irrelevant to the context in which it is found. It would be invidious to repeat the numerous criticisms that have been made of the earlier interpretations of the causal structure of displacement activities (see, for example, Hinde, 1956). They have been concerned both with the nature of the neural processes which were originally postulated or im-

¹ It must be emphasized that this is to be treated as a succession of display types only, and not as a phylogeny of the genera used as examples. On morphological grounds the relationship between *Cerodirphia* and the subgenera of *Dirphia* is almost certainly rather distant (Michener, 1952).

TABLE II. THE MAIN FEATURES OF THE DISPLAY BEHAVIOR OF 8 SPECIES OF *Dirphia* AND RELATED GENERA. All the displays are basically Type II Sustained Static Displays (Blest 1957.2) with varying degrees of modification. The orientated abdominal components when present, are used to direct the discharge of nauseous meconium from the abdominal tip towards the source of stimulation. The degree of nauseousness estimated was subjectively determined, and may not be the same for all observers.

Species	Diurnal flight threshold	Duration of display	Odor to observer	Position of antennae in display	Color and size of antennae	Abdominal orientation components
<i>Molippa simillima</i> } <i>M. latemedia</i> }	High	Sustained	Weak	Retracted against thorax	Brown; small	Absent
<i>Dirphia (Dirphiopsis) agis</i> } <i>D. (D.) eumedide</i> }	High	Sustained	Moderate	Retracted against thorax	Black; small	Absent; tip of abdomen slightly mobile in display
<i>D. (Dirphia) avia</i>	High	Sustained	Moderate-strong	Protracted and elevated to variable position	Light brown; moderate	Present, but not well or consistently sustained
<i>D. (Periphoba) hircia</i> } <i>D. (P.) sp.</i> }	Very high	Strongly sustained	Highly nauseous	Strongly elevated and orientated to stereotyped position	Lemon yellow; large	Present, sustained and well orientated
<i>Cerodirphia speciosa</i>	Very low	Absent, or occasionally transient	Moderate	Strongly elevated	Whitish; small	Absent in two transient displays

plied, and with the presence, absence or degree of available environmental or proprioceptive stimuli relevant to the release of the third "displacement" activity. Here, it is sufficient to note that the most acceptable view of displacement activities of this kind makes them formally similar to the type of Sherringtonian interaction between reflexes ("positive induction") in which the simultaneous excitation of two reciprocally inhibitory spinal reflexes lowers the threshold for the excitation of a third, by the reduction of the inhibition which the two primary reflexes would otherwise independently exert upon it (Sherrington, 1908; Kennedy, 1954; Bastock & Blest, 1958).

The best examples to date among the arthropods have concerned the appearance of displacement feeding and cleaning movements in crabs of the genus *Uca* when male sexual display is placed in conflict with escape behavior (Gordon, 1955; Crane, 1957); and, in *Drosophila melanogaster*, the appearance of irrelevant activities in the course of male courtship, under circumstances which appear to thwart the male's sexual activity (Bastock & Manning, 1955).

Other examples are not so clear-cut, and may possibly prove to be eligible as displacement behavior only under its less rigorous definitions. These include the various conflicts and their

sequels which are believed to have given rise to the protective display behavior of New World mantids (Crane, 1952), and the inappropriate responses released from male salticid spiders by stimuli resembling those which release sexual display, but which are either exaggerated or incomplete (Crane, 1949). Some of the conceptual problems arising from marginal examples of this kind have been resolved by Andrew (1956.1 & 2), who has shown that in addition to displacement behavior in the sense outlined above, animals may perform *compromise behavior* when two incompatible tendencies are aroused simultaneously. Such conflicts characteristically select certain mechanically compatible components, or even shared components of the two competing activities, and allow them expression (Andrew, 1956.1). Alternatively, one of the two tendencies may be suppressed, and the other only allowed partial expression; it is with this type of outcome that we are concerned in considering the conflict between flight and settling in the Hemileucinae. Thus the sustained antennal elevation which characterizes the incomplete settling which follows display by *D. (Periphoba) spp.* can be defined as compromise behavior resulting from the simultaneous activation of flight (suppressed) and settling (partially suppressed) behavior, and the antennal resting posi-

tion as ritualized from this ancestral conflict. The process by which this has been achieved can be legitimately included under the classical usage of the term "ritualization" (Tinbergen, 1952), because the novel position of the antennae allows them to participate in an aposematic inter-specific signal.

Finally, it is worth noting that those other genera of saturniids in which the same antennal rest-position is found are also forms in which the threshold of the flight responses appears to have been secondarily reduced. Species of *Hyalophora*, *Rothschildia* and *Epiphora* are extremely readily disturbed from rest, and it has been noted that in *H. (Callosamia) promethea* it is only in young moths that vigorous and sustained rhythmic displays can be obtained; in older moths they are abbreviated or occluded by the highly excitable flight response (Blest, 1958.2). There exists a strong probability, therefore, that this widespread antennal rest position may have been evolved through a path similar to that which has been here demonstrated for *Cerodirphia speciosa*. In conclusion, it may be emphasized that those processes which have been shown to underlie the evolution of vertebrate signal movements have counterparts in the evolution of invertebrate behavior which possess a great deal more than mere formal similarity; it is clear that the processes being studied have at least involved analogous types of causal mechanism.

V. SUMMARY

1. The settling and protective display behavior of 8 species of New World hemileucine saturniids from the genera *Molippa*, *Dirphia*, and *Cerodirphia* is described. These are: *M. simillima* Jones; *M. latemedia* (Druce); *Dirphia (Dirphia) avia* (Stoll); *Dirphia (Dirphiopsis) agis* (Cramer); *D. (D.) eumedide* (Stoll); *D. (Periphoba) hircia* (Cramer); *D. (P.)* sp. (unidentified); *Cerodirphia speciosa* (Cramer). All possess scarcely modified Type II Sustained Static Displays in which the wings are elevated and the abdomen curled so that the terminalia are approximated to the ventral surface of the thorax.

2. In one species, *Cerodirphia speciosa*, which has overtly aposematic coloration, the resting posture is aberrant; the antennae at rest are not retracted beneath the anterior margin of the forewings, but lie above the plane of the wings and along the dorsal surface of the thorax.

3. It is shown that in other species of hemileucine saturniids, this antennal position is only sustained when the full settling response is partially suppressed by an excited but covert flight

tendency; such incomplete settling responses fail to achieve the full act of antennal retraction.

4. The main behavioral adaptation of *Cerodirphia* to its over-all aposematic coloration is a lowered flight threshold linked with an unstable flight system. Unlike the other species, *Cerodirphia* will fly readily to any slight stimuli applied during daylight. Such flight responses suppress the static display, which can consequently be elicited from few individuals of the species, and then only as transient responses; in addition, settling responses must necessarily tend to be incomplete.

5. Selection, it is argued, has acted to stabilize the antennal posture reached after display, when the elevated antennal position is sustained as a result of the partial suppression of the settling response by a covertly excited flight tendency. The antennae are so enabled to participate in an aposematic resting pattern.

6. Attention is drawn to the fact that this complex interaction between three behavior patterns, natural selection, and an existing trend towards aposematic coloration, has produced an end result of a type for whose origin saltatory mutations have frequently been invoked as an explanation.

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EXPLANATION OF THE PLATE

PLATE I. *Cerodirphia speciosa* (Cramer) performing a transient display. Note the elevated antennae.